

Species composition, function and home-range of mixed-species bird flocks in a primary cloud forest in Ecuador

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Few papers have previously focused on mixed-species flocks in high-altitude humid forests (Macdonald & Henderson 1977, Moynihan 1979, Remsen 1985). Macdonald & Henderson worked in Kashmir, Moynihan described compositions of flocks from South America including central Ecuador, while Remsen focused on flock compositions in Bolivia. In this paper I present data on species composition and size of mixed-species flocks from southern Ecuador, and discuss their possible function. I also present data on the size of a flock's home-range, hitherto unknown from this altitude.

Study area

From March to May 1992 I studied mixed-species bird flocks at Cajanuma (04°06'S, 79°09'W), Podocarpus National Park, Loja Province, Ecuador. The study plot was situated in an area of temperate (montane) cloud forest at 2675–2975 m, around the park headquarters. Long periods with fog, clouds and rain prevail at Cajanuma from February to mid-October. A less wet period with some sunshine and clear sky lasts from mid-October through January (Apolo 1984, Bloch *et al.* 1991). This humid weather regime is caused by the topographic setting. Cajanuma is on the western slope of the easternmost ridge of the Andes of southern Ecuador. The altitude of the ridge above Cajanuma is only 3660 m. Hence, the weather at Cajanuma is heavily influenced by the extremely humid climate on the eastern side (Apolo 1984). The predominant vegetation is a primary cloud forest with patches of *Chusquea* bamboo on naturally- and man-disturbed slopes (Gentry 1992). The composition of trees around Cajanuma is almost the same as in the corresponding zone on the eastern slope (Madsen 1989). Epiphytes are richly developed, creating a high structural complexity and heterogeneity with many microhabitats.

Methods

Birds were mist-netted and colour-ringed for individual identification. Observations of colour-ringed individuals, and of species composition, were used to distinguish between different flocks.

The same trails were walked every day from 0600 to 1800 hrs in all kinds of weather. Flocks were observed using waterproof 10 × 42 Leica binoculars. Species were also identified by voice. I distinguished between canopy, understorey and combined flocks. In the field and when analysing the material, I distinguished between flock encounters where all species and individuals were recorded and flock encounters

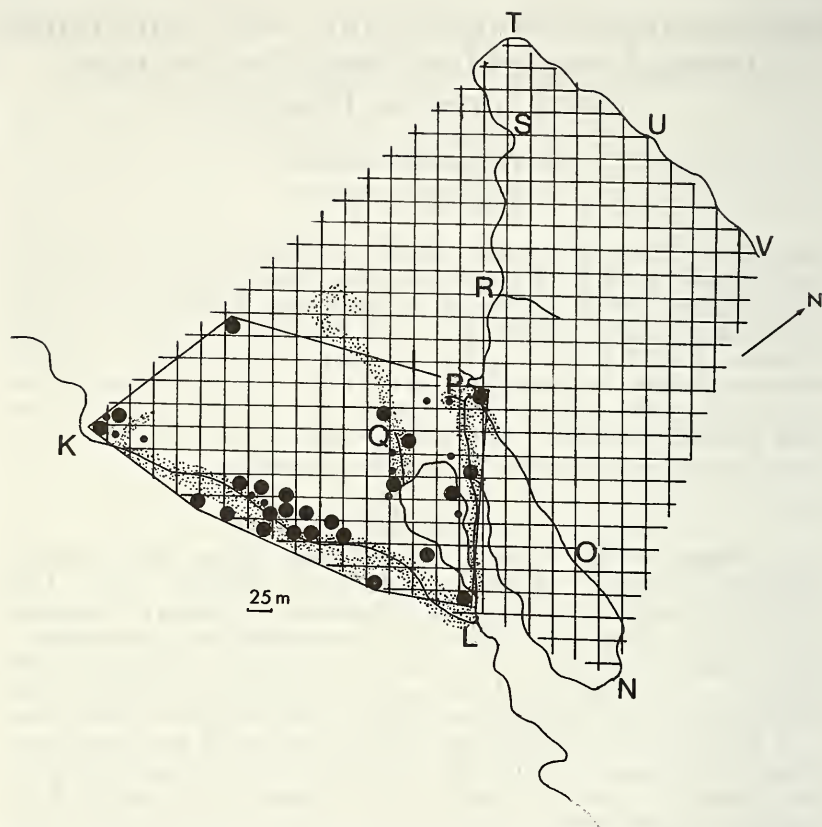


Figure 1. Map of study area at Cajanuma showing minimum principal home-range of flock A. Large dots=flocks with colour-ringed individuals; small dots=incompletely observed flocks where colour-rings were not seen, but composition similar to that of flock A; stippled=secondary scrub with bamboo.

where only some species and individuals were recorded. Due to the limited view in the forest, the majority of flock records had to be referred to the latter type. Accordingly, calculations on structure are approximations given as minimum and maximum mean numbers. For each flock encounter, the location, size and composition of the flock were recorded. To determine the locations of all encounters I used a detailed map of the area (Fig. 1), constructed by use of a bearing compass. Landmarks were established along the trails as coloured flags on poles raised high above the canopy and as colour-marks close to the ground. The approximate linear distances between the landmarks K and L and P and L on the ground were measured on the terrain, and adjustments for differences in altitude were made using trigonometric functions. Angles between the directions to various landmarks were

imposed on a gridded paper to establish reciprocal positions. Other distances were measured subsequently from the gridded map. Finally, the area of the study plot was estimated counting the grid units of Figure 1. Observations of flocks were plotted on the map to serve as a basis for calculating a minimum principal flock home-range.

Results

Birds were mist-netted during 35,911 net-metre-hours (12 m net open for 5 hrs = 60 net-metre-hours). A total of 514 birds were caught and of these, 252 potential flock-participating birds were colour-ringed. The ringed birds comprised 43 species. Altogether, 144 observations of mixed flocks, with a total of 55 different species, were made. A total of 164 observations of colour-ringed individuals were recorded.

Composition

The size of the principal study area bounded by K-T-U-V-N-L-K was c. 27 ha. Within this area at least four flocks were present. Flocks A, C and D contained species that foraged at all levels; flock B comprised only understorey species. The species composition of flock A was primarily centred around the insectivorous species Pearled Treerunner *Margarornis squamiger*, Streaked Tuftedcheek *Pseudocolaptes boissonneautii*, Blue-backed Conebill *Conirostrum sitticolor*, Grey-hooded Bush-Tanager *Cnemoscopus rubrirostris* and Black-headed Hemispingus *Hemispingus verticalis*, all with colour-ringed individuals (1, 1, 3, 2 and 2, respectively) frequently present, but the flock also contained other species attending less frequently (those with an asterisk in Appendix). None of the above mentioned colour-ringed individuals were ever seen in other flocks.

The understorey flock, B, was built around Black-capped Hemispingus *Hemispingus atropileus*, Plushcap *Catamblyrhynchus diadema*, Rufous Wren *Cinnycerthia unirufa* and Yellow-billed Cacique *Cacicus holosericeus*, but also occasionally contained Rufous-naped Brush-Finch *Atlapetes rufinucha*, Pale-naped Brush-Finch *Atlapetes pallidinucha* and Black-crested Warbler *Basileuterus nigrocristatus*. The two remaining flocks, C and D, were similar in composition to A, but with different individuals.

Many species, normally regarded as solitary (Fjeldså & Krabbe 1990), joined mixed flocks at Cajanuma. Three species of hummingbirds, Buff-winged Starfrontlet *Coeligena lutetiae*, Rainbow Starfrontlet *Coeligena iris* and Tourmaline Sunangel *Heliangelus exortis*, were seen attending mixed flocks and foraging both on insects and nectar. Even two terrestrial species, Rufous Antpitta *Grallaria rufula* and Undulated Antpitta *Grallaria squamigera*, were recorded foraging in mixed flocks. Compared to the number of observations of solitary antpittas ($n=36$) (Poulsen 1993), flock participation ($n=2$) was highly unusual. Sometimes a Great Thrush *Turdus fuscater*, Glossy-black Thrush *Turdus serranus* or Band-tailed Pigeon *Columba fasciata* suddenly found itself within a passing flock, but all three species appeared to be inactive in the flock and unaffected, and so were considered non-participants.

TABLE 1

The relative importance of different families as participants in mixed-species flocks at Cajanuma. Rank refers to the preceding column

Family	No. of flock encounters with family	% of total flock encounters (144)	Rank of family	Flock birds seen from family (A)	No. of flock species available from family (B)	Index A/B	Rank
Thraupidae	131	91.0	1	664	15	42.3	5
Parulidae	111	77.1	2	278	5	55.6	2
Coerebidae	102	70.8	3	213	5	42.6	4
Furnariidae	82	56.9	4	226	3	75.3	1
Tyrannidae	51	35.4	5	109	8	13.6	8
Fringillidae	46	32.0	6	92	2	46	3
Troglodytidae	34	23.6	7	84	2	42	6
Cotingidae	28	19.4	8	35	1	35	7
Trochilidae	8	5.6	9	8	3	2.7	12
Picidae	7	4.9	10	7	3	2.3	13
Icteridae	4	2.8	11	8	1	8	9
Dendrocolaptidae	3	2.1	12	3	1	3	11
Trogonidae	2	1.4	13	3	1	3	11
Formicariidae	2	1.4	13	2	2	1	14
Corvidae	2	1.4	13	4	1	4	10

Structure

Only 12.7% (7 of 55) of the species participating in flocks had minimum intraspecific group-sizes >2 . In some of these species, as in several non-participating species, adults were accompanied by juveniles. Many species are singing in January and March, but the song activity is also high in August–September (N. Krabbe pers. comm.). The other participating species ($n=48$) were represented only by 1–2 individuals in each flock. Thirteen of 55 species (23.6%) were regular followers (Appendix), i.e. participated in $>25\%$ of the flock encounters (Powell 1985). Ninety-one percent of all encounters included species of the family Thraupidae. More than half of the encounters also contained species of Parulidae, Coerebidae and Furnariidae (Table 1). Thraupidae had almost twice as many flock-participating species ($n=15$) as Tyrannidae ($n=8$). Considering the number of birds seen in flocks per available species (Index: A/B, Table 1), Furnariidae characterised flocks more than Parulidae, Fringillidae, Coerebidae and Thraupidae.

When the number of individuals colour-ringed was compared to the number re-sighted subsequently, striking differences appeared between three groups (Table 2). There were fewer re-sightings of colour-ringed, partially insectivorous (principally frugivorous) Thraupidae in mixed flocks than of insectivorous Thraupidae and insectivorous Furnariidae (Yates corrected $\chi^2=12.65$, $P<0.01$, f.d.=2). Understorey species difficult to observe were excluded from this calculation.

TABLE 2

The number of colour-ringed individuals and the number of subsequent re-sightings of colour-ringed individuals in mixed-species flocks for two families (three guilds) at Cajanuma

	Partially insectivorous Thraupidae	Insectivorous Thraupidae	Insectivorous Furnariidae
Colour-ringed individuals	38	6	9
Re-sightings in mixed flocks	20	14	23

As many as 76.4% ($n=110$) of all flock encounters ($n=144$) had species in all vertical layers; in only 16% ($n=23$) were the birds restricted to the canopy, and in 7.6% ($n=11$) to the understorey.

Home-range

Flock A, which comprised canopy and understorey species, used a minimum principal home-range of 8 ha (Fig. 1) with an altitudinal range of *c.* 125 m. At its largest, this flock contained at least 15 species and 27 individual birds. Flocks B, C and D roamed over areas of undetermined size from within the small loop-trail towards O, from somewhat above P towards the K-T ridge and north to somewhere between R and S, and from halfway between P-L to N and somewhere up the trail east of L, respectively.

Discussion

Structure and function

The insectivorous Furnariidae and Parulidae were the most frequent families in flocks when the number of birds seen in flocks per available species was considered (Table 1). Together with the data presented in Table 2 (fewer re-sightings in flocks of colour-ringed, partially insectivorous Thraupidae than of insectivorous Thraupidae and insectivorous Furnariidae) this suggests a looser association with mixed flocks of partially insectivorous species than of purely insectivorous species, which implies that birds join mixed-species flocks mainly to consume insects, or leave flocks to feed on other items. A negative correlation between insect activity and flocking at Cajanuma also suggests that mixed-species bird flocks form to feed on insects (Poulsen *in press*). It also creates a high degree of dynamics in flock size when widely roaming partially insectivorous birds like tanagers are constantly leaving and joining a flock.

Home-range

The ridge running from T to K was apparently a border of flock A's home-range. Flocks seen to the west side of the ridge never contained individuals with colour-rings. This was also the case with flocks observed above P. Flock A only ranged slightly below K-L (the road),

probably as a consequence of rather open forest with a lot of bamboo. A principal home-range of minimum 8 ha (flock A) is within the limits (1–10 ha) found in most studies covering humid lowland and mid-altitudes (Bushkirk *et al.* 1972, Munn & Terborgh 1979, Powell 1985). Terborgh *et al.* (1990) found at Manú in Amazonian Peru mean home-ranges of >20 ha for canopy flocks and 4–5 ha for understorey flocks (similar numbers of individuals as in Cajanuma). In this context the intermediate (between 4–5 and 20 ha) principal home-range size at Cajanuma can be explained by the flock comprising canopy as well as understorey species, and/or by use of a lower-quality forest with patches of bamboo, which necessitates the exploitation of a larger area.

Summary

Mixed-species bird flocks were studied in an Ecuadorian primary cloud forest at 2675–2975 m altitude. Birds were mist-netted and colour-ringed to permit individual identification. Considering the number of birds seen in flocks per available species, the insectivorous Furnariidae and Parulidae characterised flocks more than Fringillidae, Coerebidae and Thraupidae. There were fewer re-sightings of colour-ringed, partially insectivorous Thraupidae in mixed flocks than of insectivorous Thraupidae and insectivorous Furnariidae. Together with the families primarily characterising flocks this suggests a looser association with mixed flocks of partially insectivorous species than of purely insectivorous species, which implies that birds join mixed-species flocks mainly to consume insects. Home-range, so far unknown for flocks at this altitude, was determined by plotting flock observations on a detailed map. The best documented flock had a minimum principal home-range of 8 ha, with an altitudinal range of c. 125 m.

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APPENDIX

Species at Cajanuma seen in mixed flocks, intra-specific group-sizes given as minimum and maximum mean numbers, number of times species were recorded in flocks, and their percentages of the 144 flocks seen. Rank refers to the preceding column. *= species attending flock A less frequently than the five principal species mentioned in the text

Family and species	Average group size	Times seen in flocks	% of total	Rank
Trochilidae				
<i>Coeligena iris</i>	1.0	1	0.7	30
<i>Coeligena lutetiae</i>	1.0	4	2.8	24
<i>Heliangelus exortis</i>	1.0	3	2.1	28
Trogonidae				
<i>Trogon personatus</i>	1.5	2	1.4	29
Picidae				
<i>Veniliornis nigriceps</i>	1.0	6	4.2	25
<i>Piculus rivolii</i>	1.0	1	0.7	30
<i>Campephilus pollens</i>	2.0	1	0.7	30
Dendrocolaptidae				
<i>Lepidocolaptes affinis</i>	1.0	3	2.1	28
Furnariidae				
<i>Margarornis squamiger</i>	2.3-3.3	65	45.1	3
<i>Pseudocolaptes boissonneautii</i>	1.6-2.3	45	31.3	8
<i>Synallaxis elegantior</i>	2.0	3	2.1	28
Formicariidae				
<i>Grallaria squamigera</i>	1.0	1	0.7	30
<i>Grallaria rufula</i>	1.0	1	0.7	30

APPENDIX
Continued

Family and species	Average group size	Times seen in flocks	% of total	Rank
Cotingidae				
<i>Pipreola arcuata</i> *	1.3	28	19.4	16
Tyrannidae				
<i>Myiotheretes fumigatus</i>	1.0	2	1.4	29
<i>Ochthoeca rufipectoralis</i> *	1.3-2.0	8	5.6	23
<i>Myiophobus lintoni</i>	7.0-8.5	4	2.8	27
<i>Pyrrhomyias cinnamomea</i>	1.4-2.0	9	6.3	22
<i>Mecocerculus stictopterus</i> *	1.5-2.0	28	19.4	16
<i>Mecocerculus leucophrys</i>	1.0	1	0.7	30
<i>Phyllomyias nigrocapillus</i> *	1.0-2.0	11	7.6	20
<i>Phyllomyias uropygialis</i>	1.0	1	0.7	30
Corvidae				
<i>Cyanolyca turcosa</i>	2.0	2	1.4	29
Troglodytidae				
<i>Cinnycerthia unirufa</i>	2.6-4.3	29	20.1	15
<i>Troglodytes solstitialis</i>	1.4	5	3.5	26
<i>Thryothorus euophrys</i>	1.0	1	0.7	30
Icteridae				
<i>Cacicus holosericeus</i>	2.0	4	2.8	27
Parulidae				
<i>Dendroica fusca</i> *	1.0-2.0	8	5.6	23
<i>Myioborus melanocephalus</i> *	1.8-2.4	82	56.9	1
<i>Basileuterus nigrocristatus</i> *	1.2-2.0	46	31.9	7
<i>Basileuterus luteoviridis</i>	1.9-3.3	31	21.5	14
<i>Basileuterus coronatus</i> *	1.0-2.0	7	4.9	24
Coerebidae				
<i>Conirostrum sitticolor</i>	1.8-2.2	57	39.6	5
<i>Conirostrum albifrons</i>	1.0	2	1.4	29
<i>Diglossa albilatera</i> *	1.0	25	17.4	17
<i>Diglossa cyanea</i> *	1.2-2.0	68	47.2	2
<i>Diglossa caerulescens</i>	1.0	3	2.1	28
<i>Diglossa lafresnayii</i>	1.0	8	5.6	23
Thraupidae				
<i>Iridosornis rufivertex</i> *	1.8-2.8	37	25.7	13
<i>Anisognathus lacrymosus</i> *	1.4-2.0	60	41.7	4
<i>Anisognathus igniventris</i> *	1.7-2.0	10	6.9	21
<i>Buthraupis eximia</i>	1.0	2	1.4	29
<i>Buthraupis montana</i> *	2.4-3.6	17	11.8	19
<i>Chlorornis riefferii</i>	1.7-2.3	9	6.3	22
<i>Dubusia taeniata</i>	1.5-2.0	17	11.8	19
<i>Tangara vassorii</i> *	1.4-2.3	47	32.6	6
<i>Thraupis cyanocephala</i>	1.8	4	2.8	47
<i>Piranga rubriceps</i>	1.0	2	1.4	29
<i>Chlorophonia pyrrhophrys</i>	1.5	4	2.8	27
<i>Cnemoscopus rubrirostris</i>	2.2-3.7	41	28.5	10
<i>Hemispingus verticalis</i>	2.3-3.6	40	27.8	11
<i>Hemispingus atropileus</i>	3.2-3.8	39	27.1	12
<i>Catamblyrhynchus diadema</i>	1.4-2.0	18	12.5	18
Fringillidae				
<i>Atlapetes rufinucha</i> *	1.6-2.1	43	29.9	9
<i>Atlapetes pallidinucha</i>	1.8-3.0	14	9.7	20